WORLD COTTON RESEARCH CONFERENCE-3

COTTON PRODUCTION FOR THE NEW MILLENNIUM

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Genome mapping of tetraploid cotton: Towards a saturated and unified map

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ABSTRACT

DNA-based genetic maps have been produced in nearly all major crop species, thus facilitating the analysis of genome structure and evolution, and improving efficiency and accuracy of breeding. We have developed at Cirad/France a combined and saturated RFLP-AFLP-SSR genetic map of tetraploid cotton from the analysis of the 1st and 2nd backcross generations of an interspecific Gossypium hirsutum *(cv 'Guazuncho 2') x G.* barbadense *(cv 'VH8') cross. The BC1 and BC2 maps were independently constructed from the analysis of 75 and 200 individual plants respectively. As a recent development, a microsatellite-enriched library had been developed and 418 new microsatellite primers defined. One hundred and sixty one microsatellites showing at least one polymorphism between Guazuncho 2 and VH8 had been screened on the BC1 population, and 185 new loci were added on the BC1 map. Having 360 loci in common between the BC1 (1107 loci in total) and the BC2 (513 loci in total) map proved helpful to confirm loci orders along linkage groups, and allowed small linkage groups to be joined to larger ones. A total of 138 additional loci, mainly AFLP, of the BC2 map were added to the skeleton BC1 map. Finally, after merging the BC1 and BC2 mapping data, the Guazuncho 2 x VH8 map now comprises 1260 loci divided mainly between AFLPs (40%), SSRs (34%) and RFLPs (15%). The 26 linkage groups span altogether over 5400 cM. Details of the Guazuncho 2 x VH8 map are commented. An important number of microsatellite and RFLP markers used in the present study are common with other published genetic maps also derived from interspecific* G. hirsutum *x* G. barbadense *populations. As a preliminary step towards an integration of the different maps, we used a "neighbor approach" applied to 4 of the 26 chromosomes by aligning these maps using these bridge loci. An overall agreement in locus order and distances has been observed. Integration of genetic maps into a denser consensus unified map of tetraploid cotton and future feasibility of genetic and physical maps integration are discussed.*

Introduction

The construction of molecular linkage maps has become an essential tool for plant molecular genetics and breeding research. Several ongoing efforts worldwide are devoted to developing marker-assisted breeding and promoting molecular tools and genetic engineering strategies in cotton. Different published or in-development maps derive either from diploid genomes (Brubaker, *et al*., 1999), from tetraploid *Gossypium hirsutum* intraspecific crosses (Shappley, *et al*., 1998; Ulloa, *et al*., 2002), or from interspecific *G. hirsutum* x *G. barbadense* populations (Reinish, *et al*., 1994; Zhang, *et al*., 2002; Lacape, *et al*., 2003). The RFLP map reported in Reinish *et al*. (1994) derives from an F_2 population of cross *G. hirsutum* race palmeri x *G. barbadense* (cv. K101). It had recently been extended as reported at http://www.plantgenome.uga.edu/cotton/GeneticMap.htm (University of Georgia, USA), allowing the mapping of over 3000 loci, the majority of which are RFLPs, along 26 linkage groups spanning 4550 cM. The population mapped by Zhang *et al*. (2002) originates from haploid and double-haploid plants of the TM1 x Hai 7124 cross. In that map, 489 SSRs and RAPDs loci were assembled into 43 linkage groups covering 3315 cM. Though not published, but partially available from the CottonDB web site at http://ukcrop.net/perl/ace/search/CottonDB, two other interspecific F_2 maps, namely TM1 x 3-79 with 868 loci, 50 linkage groups, and 5000 cM according to Yu and Kohel (2001); and TM1 x NM24016, have also been developed. Cirad/France recently extended the combined RFLP-AFLP-SSR genetic map of the Guazuncho 2 x VH8 BC1 population (Lacape, *et al*., 2003) after aligning it with the BC2 generation map and after integrating newly developed SSR loci and fiber quality candidate genes. The present communication reports primarily on the updated status of the Guazuncho 2 x VH8 map. Secondly and after aligning the Guazuncho 2 x VH8 map with other existing genetic maps using RFLP and SSR bridge loci, we assess the feasibility of an integration of genetic maps in tetraploid cotton. Case examples of four linkage groups are further developed.

Experimental procedure

Plant material

The BC1 (backcross to the *G. hirsutum* parent) population, grown at Montpellier in 1999, was composed of 75 plants, and originated from a Guazuncho 2 x VH8-4602 cross. 'Guazuncho 2' is a modern pure-line *G. hirsutum* variety developed in Argentina. The 'VH8-4602' *G. barbadense* parent originates from Antigua and derives from a cross between 2 'Sea Island' types. The BC2 (2nd backcross to the *G. hirsutum* parent) population was grown under field conditions during summer 2000 (May-October) in Montpellier, and comprised 200 individual plants originating from 51 different BC1 plants.

Molecular analysis

Molecular markers used in this study included RFLPs, SSRs and AFLPs. Using the 147 RFLP probes developed by A. Paterson (University of Georgia) that showed at least one polymorphism between our par-

ents, 174 segregating loci were identified. These RFLP probes were common to the ones mapped on the palmeri x K101 population (Reinish, *et al*. 1994). Microsatellite markers used were of two types. The collection of 216 Brookhaven National Laboratory (prefix BNL) SSRs was screened for polymorphism on our parents and a total of 179 SSRs revealed 230 loci. Secondly, a $(CA)_n$ microsatellite-enriched genomic library was recently developed at Cirad. The method was based on the hybridization of biotin-labelled oligoprobes on digested genomic DNA followed by a capture of selected sequences with streptavidin-coated magnetic beads, following the protocol described in Billotte *et al.* (1999). Of the 418 microsatellites for which primer pairs had been designed, 304 have so far been tested (activity still in progress). A total of 151 of the 304 (50%) SSRs have shown at least a single polymorphism between parental species, and 185 additional loci (these are further referred as "CIR") have been added to the BC1 map. AFLP analysis was performed using the Life Technology AFLP™ analysis system I (Gibco BRL, Gathersburg, Md., USA) using the total set of 64 *Eco*RI/*Mse*I combinations (8 *Eco*RI and 8 *Mse*I primers) for the BC1 DNAs, and a subset of 45 pairs for the BC2 DNAs. The selected subsets of SSRs (81 BNL primer pairs) and of AFLPs pairs used to analyze the 200 BC2 individual plants were chosen for their even distribution along the 26 chromosomes of the BC1 map. RFLP, SSR, and AFLP protocols were as described in Lacape *et al.* (2003).

Overall, the allelic contributions (either homozygote for *G. hirsutum* alleles, or heterozygote *G. hirsutum*/*G. barbadense* alleles) in the BC1 and BC2 generations, were finally scored for 465 AFLPs, 229 SSRs, 192 RFLPs, and 2 morphological markers on the 75 BC1 plants, totalling 1014 loci (of which 888 mapped), and for 147 SSRs and 447 AFLPs, totalling 594 loci (of which 513 mapped) on the 200 BC2 plants.

Mapping analysis of BC2 population and integration of BC1 and BC2 maps

Mapmaker software (successively applying the commands 'group' at LOD>5, Rf = 30 cM, and Kosambi cM, 'try' and 'ripple') was used for positioning new CIR loci on the existing BC1map and for constructing the BC2 map. The BC2 map was then aligned with the BC1 map.

Integration of four independent G. hirsutum x G. barbadense maps

Apart from the Guazuncho 2 x VH8, further referred to as GV map, three other genetic maps as reported from the literature or from the web resources were compared. The chromosomes and groups of the palmeri x K101 map, referred to as PK map, were rebuilt from pdf chromosome images shown at the University of Georgia website. The map published by Zhang *et al.* (2002), will be further referred to as "TH". Lastly, as some linkage groups of the TM1 x 3-79 and TM1 x NM24016 maps had already been integrated as reported from the CottonDB website, we considered these mapping data as pooled data and will refer to them as "T3+TN". Linkage groups and chromosomes from the different maps could be unambiguously reassembled using common loci: i.e. RFLPs and BNL microsatellites between PK and GV, and BNL microsatellites between all maps. We used the linkage groups and chromosomes nomenclature as proposed in Lacape *et al.* (2003). Examples of 4 groups, c1, c15, A03, and D02, were considered in this preliminary approach.

Results

Updated status of the combined RFLP-SSR-AFLP map of Guazuncho 2 x VH8 BC1 population

The 185 new microsatellites "CIR" loci mapped along all 26 chromosomes of the BC1 map (between 2 on c9 and 16 on D04) (Table 1). For 16 of the 26 chromosomes, at least one new locus mapped to a distal part explaining the overall increase of 700 cM between the 4700 cM in Lacape *et al.* (2003) and present 5400 cM (Table 1). Though not detailed in this presentation, 34 additional loci referred as "candidate genes" for fiber elongation were also mapped. The BC1 map comprises 1107 loci mapped along 26 long linkage groups and 3 small unlinked groups. The total distance of 5400 cM is not accounting for gaps to be filled for bridging the 3 small groups. Three small groups, NL3, NL5 and NL6, comprising nine loci and covering 76.8 cM, remain unassigned, while three previously unassigned groups (NL1, NL2 and NL4) have been merged to larger ones. The 13 A and D subgroups of chromosomes account for 610 loci (2903 cM) and 488 loci (2420 cM) respectively.

Combined AFLP/SSR BC2 map and integration of BC1 and BC2 maps

Apart from 81 unlinked loci, the BC2 map (not shown) comprises 513 loci mapped along 26 linkage groups spanning 3150 cM. Each BC2 group was bridged to a corresponding chromosome of the BC1 map by an average of 16 common (between nine and 37) AFLP or SSR loci, making a total of 360 common bridge loci (see Figure 1 for examples of four chromosomes). The two maps independently constructed from the two populations fully agreed in locus orders, though distances between common loci were frequently reduced in the BC2 map as compared to the BC1 map (Figure 1). Interestingly, the five cases of loose linkages between a short and a long linkage group observed on the BC1 map were all confirmed thanks to the BC2 data. Finally, 153 additional loci (149 AFLPs and 4 SSRs) initially not scored on the BC1, were mapped on the BC2 population.

After adding the new CIR microsatellites (185),

new candidate genes (34) and additional loci of the BC2 map (153), the final BC1/BC2 consensus map comprises 1260 loci divided between AFLPs (597 or 40%), SSRs (419 or 34%), cotton RFLPs (191 or 15%), *Arabidopsis* RFLPs (11 loci), candidate genes for fiber elongation (42 loci), and two morphological markers.

Integration of independent G. hirsutum x G. barbadense maps

By the use of common SSRs ('BNL' type) mapped on all populations, and of RFLPs mapped on PK and GV populations, different maps were tentatively aligned. Table 2 summarizes the comparative number of loci and distances per chromosome from different populations, using chromosome designations proposed in a previous paper (Lacape *et al*., 2003). The comparative maps of four chromosomes arbitrarily chosen as graphical examples are depicted in Figure 2.

Case example of chromosome 1 Eight loci (six RFLPs and two SSRs) are common to the GV and PK maps, while five and four BNLs bridge the GV map to TH, and the TH map to T3+TN maps respectively. Two inversions are caused by the relative positions of pAR077 (GV and PK) and BNL1667 loci (TH and T3+TN). Considering both common loci and loci unique to either PK (82 loci), GV (19), TH (9), and T3+TN (2) maps, a total of 123 different loci can be inferred as belonging to c1. An average distance of 1.5 cM between two loci would be reached if taking the longest length (183 cM on GV) into account.

Case example of chromosome 15 Inversions are caused by relative positions of A1553 (PK and GV) and BNL3090 on the TH map. The twelve loci common to either two or three maps, and the 131 unique loci (PK: 91, GV: 20, TH: 13, and T3+TN: 7) make a total of 144 loci mapped on c15, and a 1.4 cM average distance between loci.

Case example of linkage group A03 The A03 groups have 13 loci in common between GV and PK maps, 15 between GV and TH maps, and five between TH and T3+TN maps. Loci orders are congruent except for an inversion caused by the relative placements of BNL2632a and BNL3254 on TH and T3+TN. Of the 74 loci mapped on GV, 52 are unique. There are 97 unique loci on PK, 8 on T3+TN, and 8 on TH. Overall, 142 different loci are mapped on A03 for a maximal length of 271 cM and an average distance of 1.9 cM between loci.

Case example of linkage group D02 A total of 20 loci bridge the different maps, with no inversion. These common loci, added to the unique loci of PK (124 loci), GV (46), TH (1) and T3+TN (6) maps, make a total 197 loci mapped along 290 cM of D02, and an average 1.5 cM distance between loci.

Discussion

The maps of different independent *G. hirsutum* x *G. barbadense* populations were aligned and tentatively integrated using common RFLP and SSR loci. Apart from few minor inversions in marker orders and local discrepancies in distances (data not shown except for four chromosomes), the different genetic maps proved highly congruent. Although the mapping data that has been explored were partial data, and considering that numerous on-going efforts in genetic mapping from both public and private bodies are developed worldwide, one may be optimistic that map integration in cotton will be feasible. The data we surveyed indicate that an integration of genetic maps of tetraploid cotton would result in an overall recombination length of 5400-5600 cM. This overall length is clearly accounted for by a series of 26 long linkage groups or chromosomes, ie average length per chromosome is over 200 cM, and possibly a small (100 cM) additional recombinational distance attributable to unlinked groups. Total number of unique loci cumulated over the different maps is probably over 4000, meaning that marker density of a consensus map would be between 1.3 to 1.5 cM between loci.

Apart from the rice and *Arabidopsis thaliana* model plant genomes, integrated mapping is underway for different plant species, including sorghum (Menz *et al*., 2002), maize (Cone *et al*., 2002), ryegrass (Armstead *et al*., 2002), sunflower (Yu *et al*., 2003) or *Brassica oleracea* (Hu *et al*., 1998). Though RFLPs and SSRs had been recognized as reference markers for comparative mapping, the allele specificity of AFLP markers (Rouppe van der Voort *et al*., 1997), and their possible conversion to locus specific co-dominant markers (Negi *et al*., 2000; Xu *et al*., 2001) possibly expand their usefulness in genetic applications. In our case, the AFLP available from the GV population represented ca 40% of the loci. These AFLPs could not be used for map alignment, although (i) the TM1 x 3-79 map was reported as comprising 267 AFLPs (cited in Yu and Kohel, 2001, not published), and (ii) our AFLP screening included both TM1 and 3-79 DNAs as controls, allowing for a possible cross referencing of AFLP loci.

The integration of genetic, and therefore of physical, resources in cotton however represents a complex challenge. The genome is large (2200-3000 Mb and 400-500 kb per cM), it is laden by important amount of repetitive DNA (Zhao, *et al*.. 1995), and, due to polyploidy, virtually all markers occur at two or more unlinked loci (Reinish *et al*., 1994; Lacape *et al*., 2003). The task of integrated mapping implies an important amount of practical core information to be gathered, like method used for calculating map distances, confidence levels (LOD score) of marker orders, exact and unambiguous description of markers and loci. Although the examination of some case examples have demonstrated a clear cross referencing of individual loci and linkage groups from different genetic maps, the "cotton mapping" research community will soon need to communally define a consensus list for common loci, linkage groups and chromosomes denominations. The adoption of a public reference mapping population in cotton might not be necessary, once individual maps

contain a sufficient number of bridged loci that had been confidently mapped. One may also recommend some concerted supplementary mapping efforts be undertaken for increasing the number of bridge loci, and for solving some particular cases of apparent contradictions. The development and future mapping of numerous supplementary SSR loci, including those derived from the set of 418 SSR of Cirad but also from those 305 reported in Reddy *et al*. (2001) and over 1200 reported in Kumpatla *et al*. (2002), will also help define sets of chromosome-specific markers being evenly partitioned and highly informative if multiplexed. In the longer term such coordinated efforts for an integration of genetic and physical resources of cotton, possibly in the framework of the International Cotton Genome Initiative, ICGI, will serve as a foundation for fine mapping and map-based cloning of genes of interest.

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Table 1. *Status of the Guazuncho 2 x VH8 genetic map: data per chromosome and groups of A/D chromosome subsets. "CIR" loci refer to additional microsatellite loci mapped from Cirad enriched library (activity still in progress).*

Chromosome	BC1 map[1] Nb loci	BC1 map[1] Length cM	Additional "CIR" loci on BC1 map	Additional BC2 loci on BC1 map	Updated BC1/BC2 map Nb loci[2]	Updated BC1/BC2 map (Length cM
c1	23	155.7	7	1	35	182.9
c15	30	155.9	9	1	41	202.7
c2	38	172.3	1	10	49	175.6
c14	31	149.1	11	2	45	197.4
c3	36	130.6	9	3	48	156.6
c17	22	80.8	4	4	32	90.3
c4	26	126.7	9	6	43	190.2
c22	20	103.4	7	1	30	139.4
c5	38	225.2	11	8	58	290.9
D04	35	211.9	16	4	57	228.5
c6	36	259.5	10	13	59	332.2
c25	33	174.2	5	9	48	180.7
c7	39	151.6	4	5	50	189.5
c16	17	128.8	3	2	22	186.4
c9	38	287.9	2	6	49	313.1
c23	30	168.9	5	2	39	173.1
c10	32	132.1	5	10	47	133.2
c20	28	208.2	9	1	38	241.8
c12	48	205.8	7	12	68	186.8
c26	21	124.2	10		32	195.6
A01	49	178.2	7	5	62	237.8
c18	37	162.6	5	5	48	158.0
A02	50	225	5	18	74	242.2
D03	32	141.8	5	8	46	135.1
A03	54	248.7	8	11	74	272.0
D02	32	254.3	9	6	51	291.2
NL	13	104.7	2		15	76.8
Total A	507	2499.3	85	108	716	2903.0
Total D	368	2064.1	98	45	529	2420.2
TOTAL	888	4668.1	185	153	1260	5400.0

[1] As in Lacape *et al.* (2003)

[2] Including fiber elongation candidate genes (not published).

Table 2. *Comparative mapping in tetraploid cotton. Mapping data from 4 different interspecific* G. hirsutum *x* G. barbadense *populations. Chromosome nomenclature is based on Lacape et al (2003). Linkage groups and chromosomes correspondence between* palmeri *x K101 and Guazuncho 2 x VH8 maps are supported by an important number of common loci. Correspondences of TM1 x Hai 7124 and TM1 x 3-79/NM24016 are indicative.*

Cross	Palmeri x K101 [1]		Guazuncho2 x VH8 [2]		TM1 x HAI 7124 [3]		TM1 x 3-79 [4] TM1 x NM24016	
Chromosome	Loci	cM	Loci	cM	Loci	cM	Loci	cM
c1	90	157.5	35	182.9	15	152.0	6	69.0
c15	97	196.0	41	202.7	20	190.3	11	103.8
c2	67	152.0	49	175.6	19	230.4	4	35.0
c14	124	177.4	45	197.4	13	163.1	7	90.0
c3	109	194.8	48	156.6	8	94.3	21	240.0
c17	59	84.0	32	90.3			6	80.0
c4	133	243.0	43	190.2	6	57.9	5	130.0
c22	62	94.7	30	139.4	8	85.3	4	60.0
c5	172	266.2	58	290.9	5	30.2	6	80.0
D04	171	271.1	57	228.5	11	102.1	12	100.0
c6	71	125.1	59	332.2	6	56.4	8	160.0
c25	88	166.9	48	180.7	15	87.4	8	85.0
c7	87	149.0	50	189.5	18	238.8	2	23.0
c16	87	150.6	22	186.4			3	30.0
c9	99	166.9	49	313.1	18	151.8	11	85.0
c23	78	135.0	39	173.1	10	102.6	4	80.0
c10	110	183.4	47	133.2	8	90.8	7	105.0
c20	89	146.2	38	241.8	10	105.0	10	85.0
c12			68	186.8	13	116.3	14	170.0
c26			32	195.6			5	80.0
A01			62	237.8	10	98.1	6	40.0
c18	101	160.1	48	158.0	11	69.0	8	65.0
A02	103	188.8	74	242.2	6	42.7	15	200.0
D03	97	192.9	46	135.1	12	101.6	7	125.0
A03	105	198.8	74	272.0	24	219.8	19	145.0
D02	134	182.2	51	291.2	9	199.0	17	186.0
Unknown			15	76.8	39	309.9	3	150.0

[1]Data adapted from http://www.plantgenome.uga.edu/cotton/GeneticMap.htm

[2]Data updated from Lacape *et al.* (2003)

[3]Data adapted from Zhang *et al.* (2002)

[4]Data adapted from http://ukcrop.net/perl/ace/search/CottonDB - from either TM1x3-79, M1xNM24016, or both

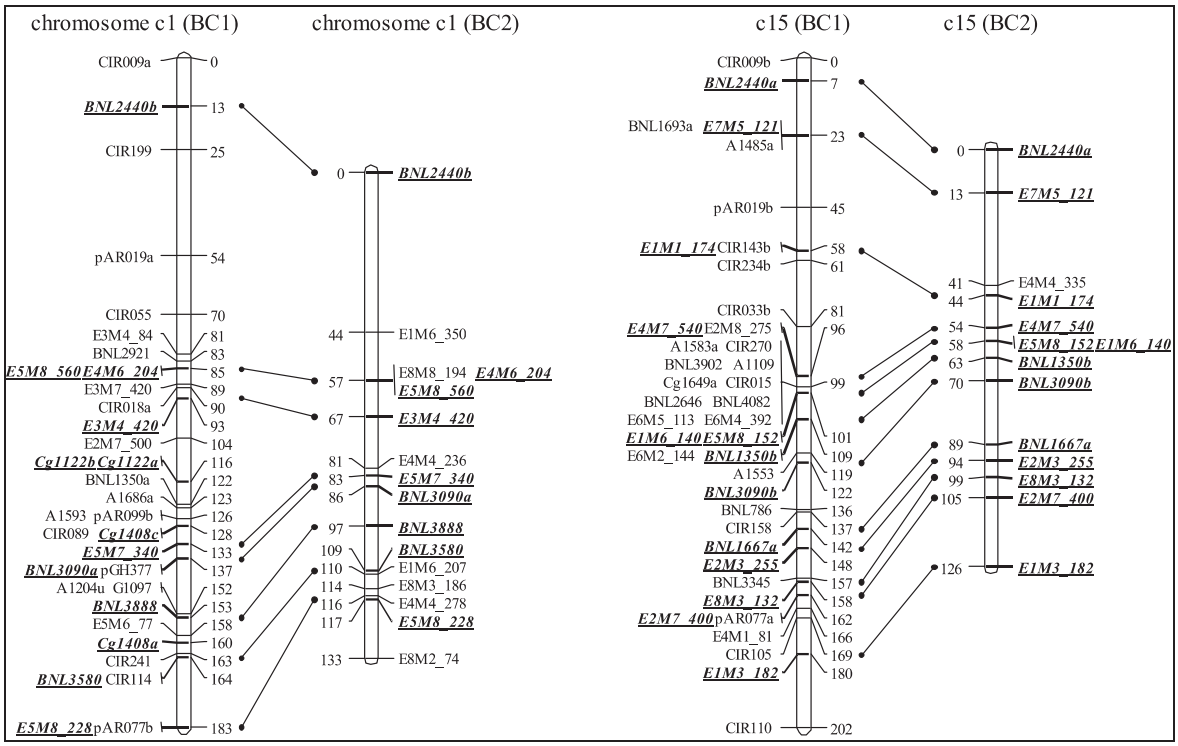

Figure 1.

Alignment of BC1 and BC2 maps from Guazuncho 2 x VH8 cross: examples of chromosomes c1 and c15. Loci common (in bold, italicized and underlined) to the BC1 and BC2 maps are connected.

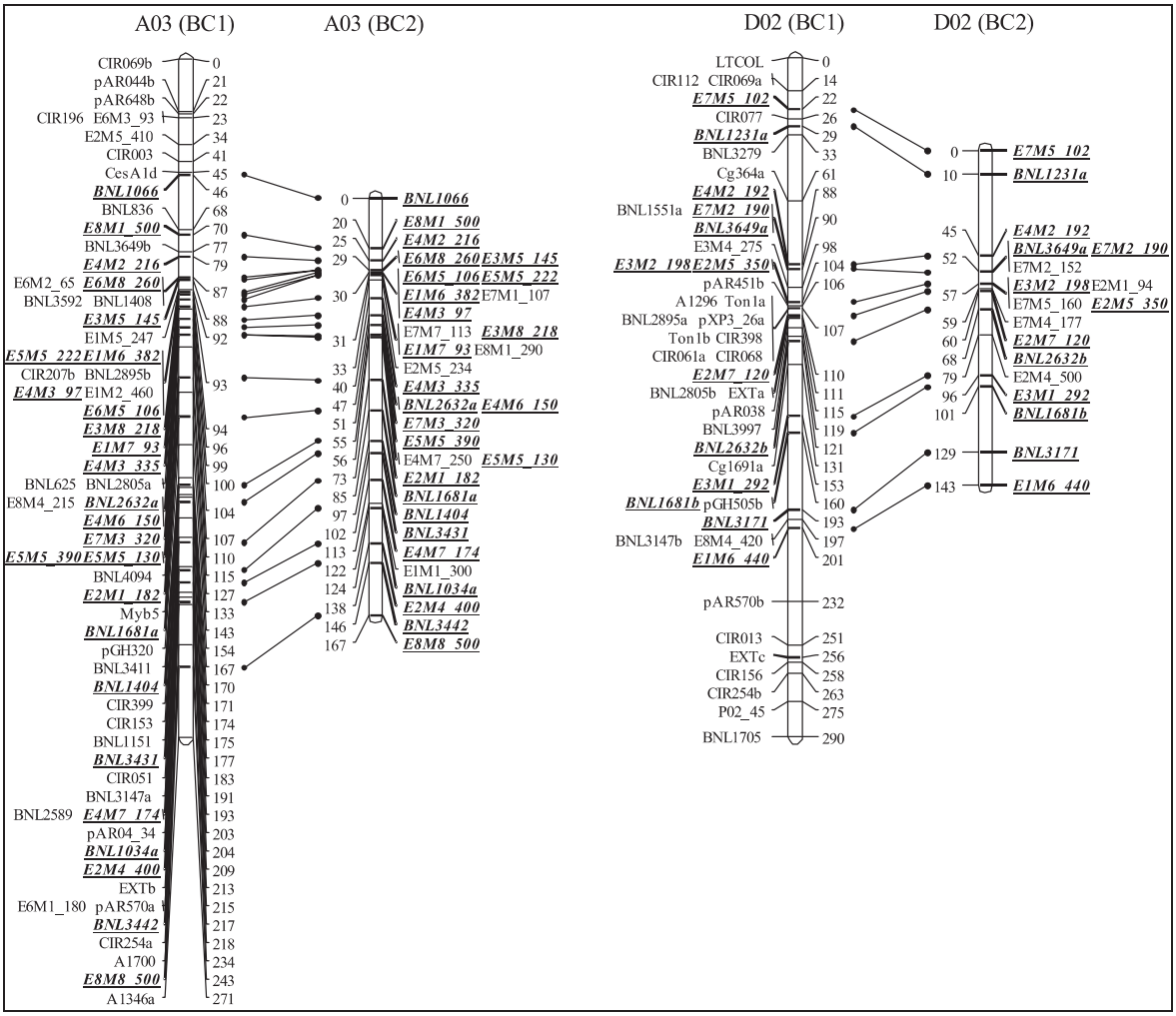

Figure 1 (contd).

Alignment of BC1 and BC2 maps: examples of linkage groups A03 and D02.

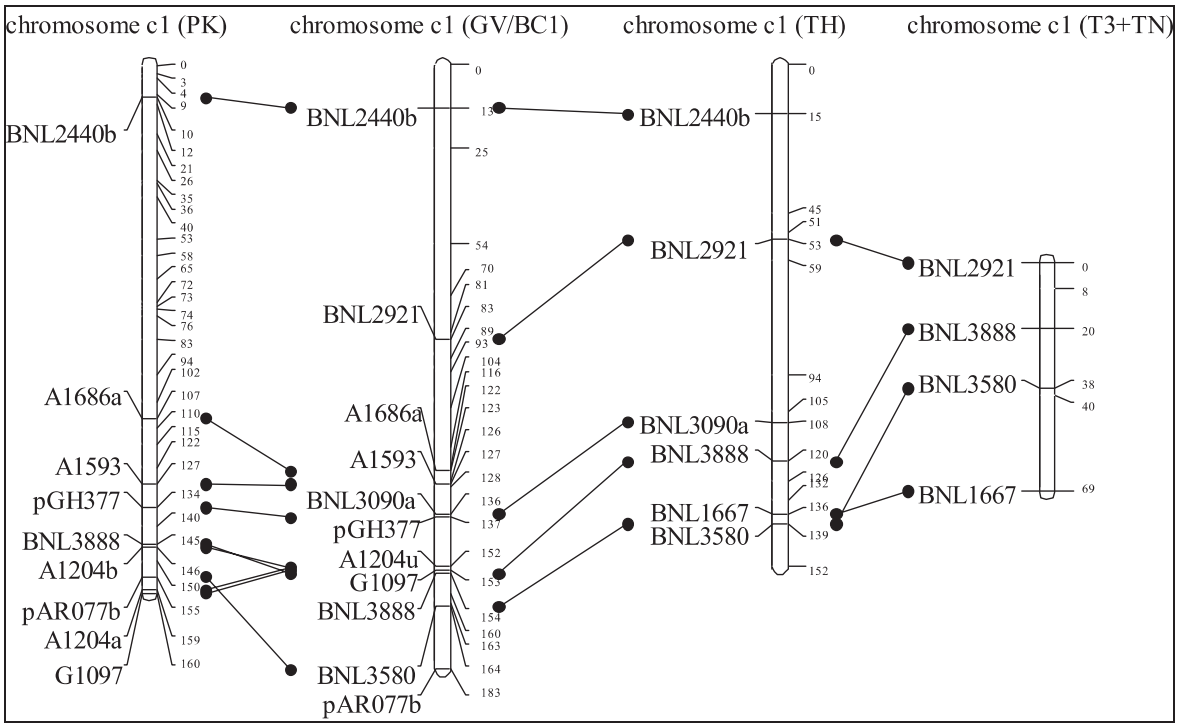

Figure 2.
Linkage group alignments of different genetic maps (see text for details): Example of chromosome 1. The loci common between at least two of the four maps are shown and connected when groups are adjacent. Locations of unique loci along groups are shown by their position in cM units. Map acronyms (PK for palmeri *x K101, GV for Guazuncho 2 x VH8, TH for TM1 x Hai 7124, T3+TN for combined data of TM1 x 3-79 and TM1 x NM24016) and chromosome designation, when different in source text as from that indicated, are mentioned in brackets.*

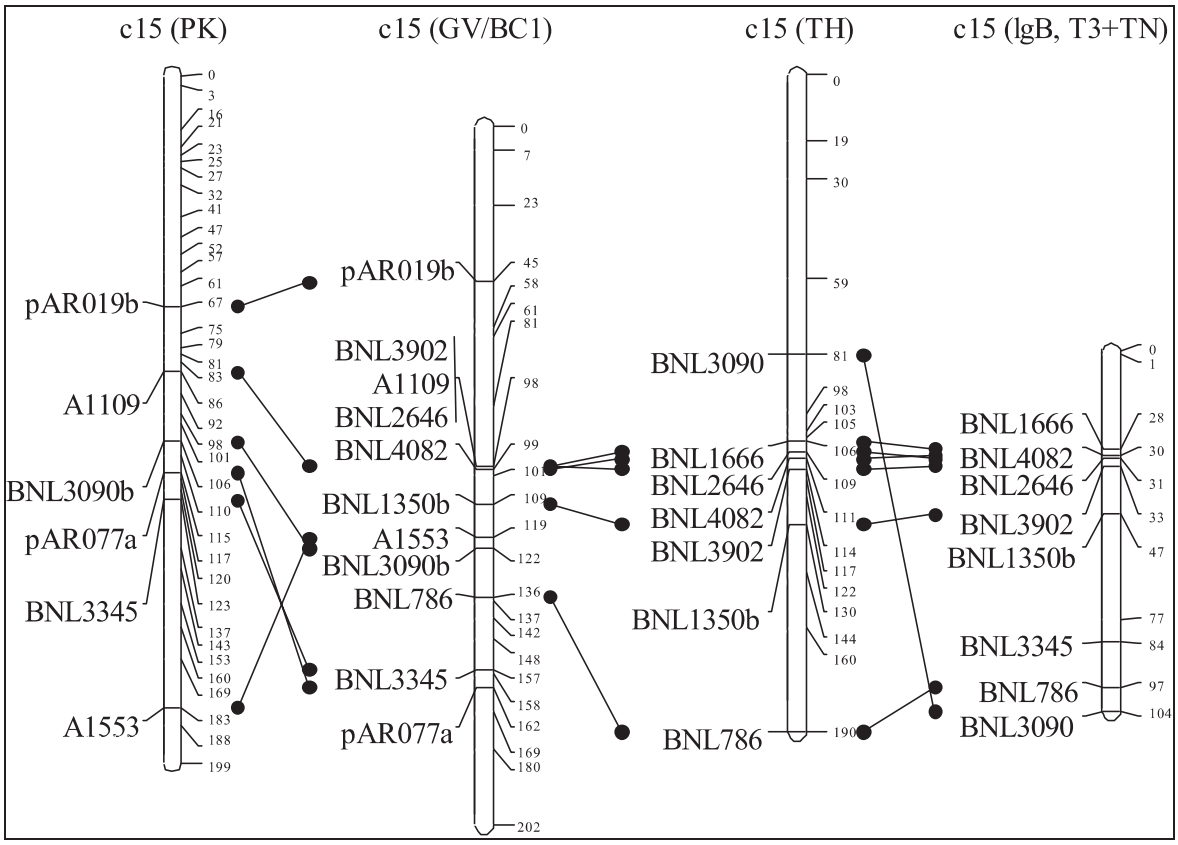

Figure 2 (contd).
Example of chromosome 15.

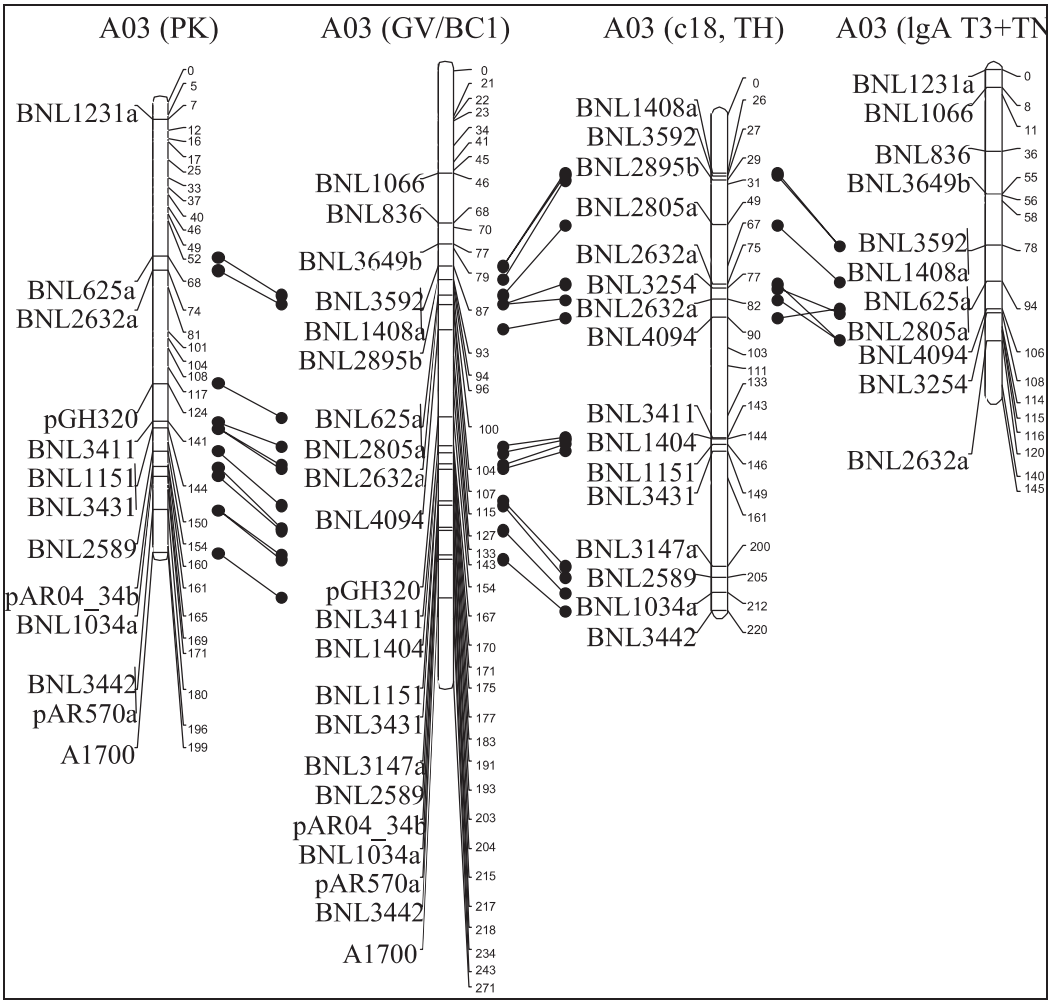

Figure 2 (contd).
Example of linkage group A03.

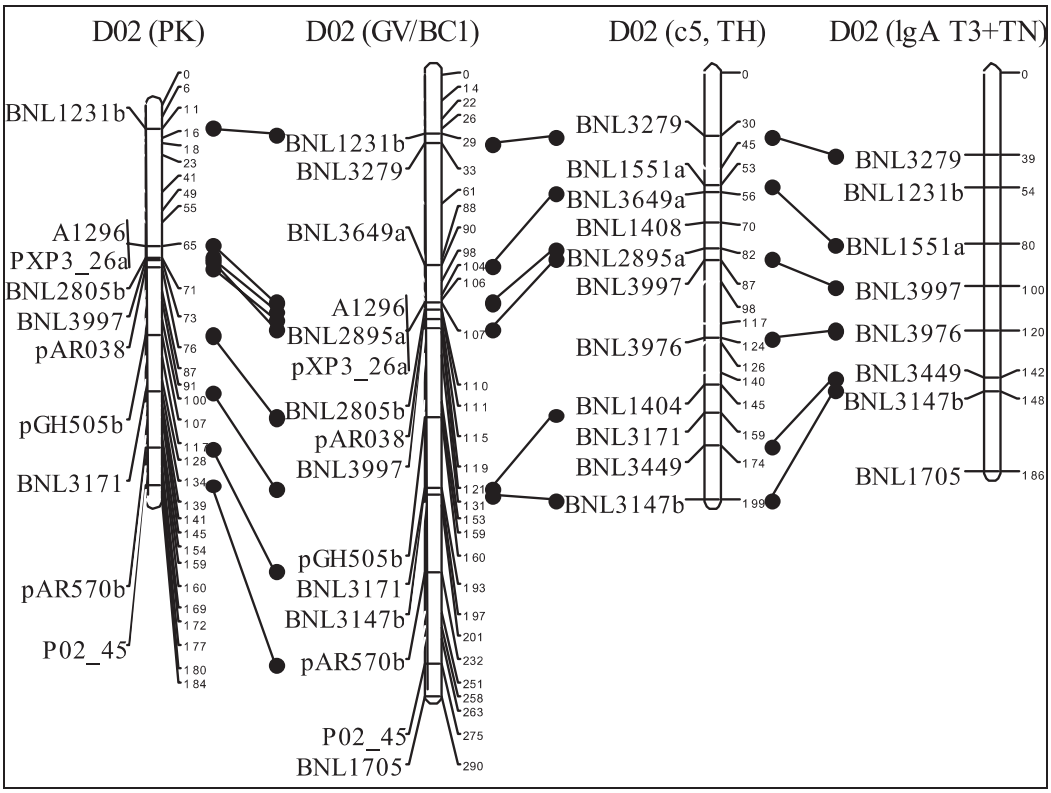

Figure 2 (contd).
Example of linkage group D02.